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UCA PANACEA, A NEW SPECIES OF FIDDLER CRAB
FROM THE GULF COAST OF THE UNITED STATES

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This paper documents the presence of a new species of fiddler crab, *Uca panacea*, on the Gulf Coast of the United States. A morphological description of the larval and adult specimens is given here, with special reference to those characters which distinguish the new form from *U. pugilator*, with which it has been confused.

Most of the North American fiddler crabs (Genus *Uca*) are found along the Atlantic and Gulf Coasts of the United States. Rathbun (1918) first attempted to list all of these species and describe them. She listed 9 species, including *Uca pugilator* (Bosc), the most common form, which is found from Cape Cod, Mass., to Florida and along the Gulf Coast to Texas.

Since her initial study, some new species have been described. Tashian and Vernberg (1958) designated *U. pugnax* and *U. rapax* (considered by Rathbun to be subspecies) as distinct species. Salmon and Atsides (1968) described two new species, *U. longisignalis* and *U. virens*, as distinct from the Atlantic populations of *U. pugnax* with which they had previously been confused. Subsequently, these findings were confirmed by Selander, Johnson and Avise (1971) employing as their measure electrophoretic analyses of variation in muscle proteins.

Rao and Fingerman (1968) described two variants in coloration pattern among "*U. pugilator*" from the Panacea area. Each variant exhibited different chromatophoric response to

black and white backgrounds. The study by Selander, et al. (1971) led to the discovery that Gulf Coast specimens, thought to be *U. pugilator*, could be placed in two distinct groups. That finding led to this morphological study. In another paper (in preparation), behavioral differences between the two forms are considered. The results indicate that *U. panacea* new species exists sympatrically but distinct from *U. pugilator* on the Gulf Coast of the United States.

METHODS

Uca panacea new species was found and studied within a ten-mile radius of the Florida State University Marine Laboratory, Carrabelle, Florida. Several large populations were found on the beach areas of Saint Mark's wildlife preserve, just east of Panacea, Florida. Animals from this location were used in this study.

About 150 individuals were collected and brought back alive to the University of Illinois, Urbana. The sample consisted of males and females from 1.1 to 1.8 cm in carapace width. The crabs were maintained in a large, 400 liter aquarium, 1.9 m long by 58 cm wide), provided with a bank of sand. These crabs, which were observed for behavioral studies, were also measured.

Characters measured with vernier calipers (accurate to 0.01 mm) were the following: width of front; width of carapace at its greatest dorsolateral extension; on large chela—length of propodus (from tip of finger to proximal edge), dactyl length (from tip to upper point of articulation with propodus), and dactyl width from ventral tooth ridge to dorsal margin midway from tip to point of articulation with propodus. Regressions for these measures were established for each species. The figures were then subjected to statistical analysis by comparison of regression slopes. In other cases, means of certain measurements were compared, using a *t*-test. The 0.05 level was chosen to reject the null hypothesis of no significant difference between the samples.

The number, distribution, and form of the spoon-tipped hairs on the merus of the second maxilliped were examined. Samples of 14 maxillipeds from 10 males and 4 females from

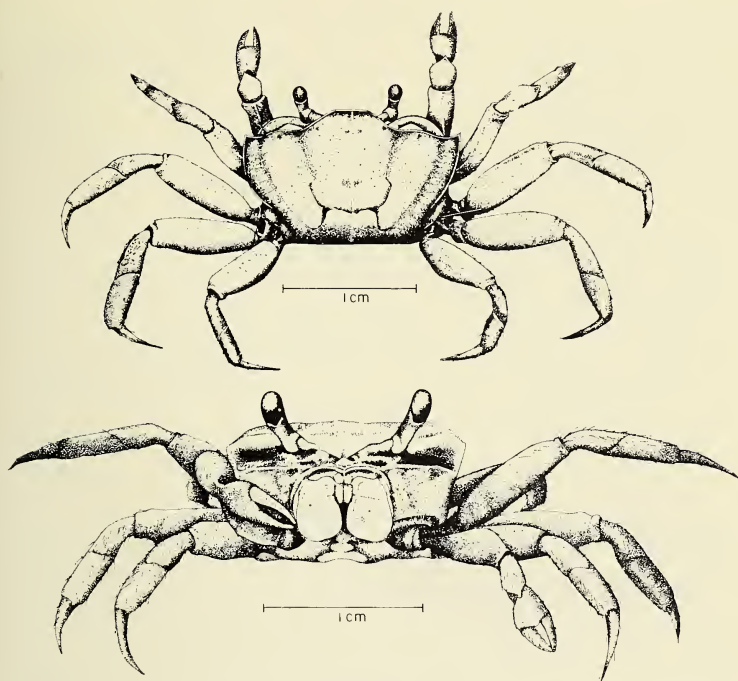


FIG. 1. *Uca panacea*, new species, allotype female. Top, dorsal view; bottom, frontal view.

U. panacea new species were photographed and compared to 4 maxillipeds from *U. pugilator*, as well as previous descriptions of the latter (Miller, 1961). The hair tips for both species were photographed under a scanning electron microscope (magnification 450–900 \times). Hairs used for electron microscopy were taken from fresh maxillipeds that had been placed in 95% ethyl alcohol for at least 72 hours. The hairs were mounted on pedestals and gold-palladium coated in a vacuum chamber before being photographed.

Five egg-bearing females were sent to the Duke University Marine Laboratory, Beaufort, North Carolina. The larvae were reared to the second crab stage at a temperature of 25 degrees C, salinity of 35 ppt, and photoperiod 12 L: 12 D, using established techniques (Costlow and Bookhout, 1962). A few (10–20) larvae at each stage were preserved in a solu-

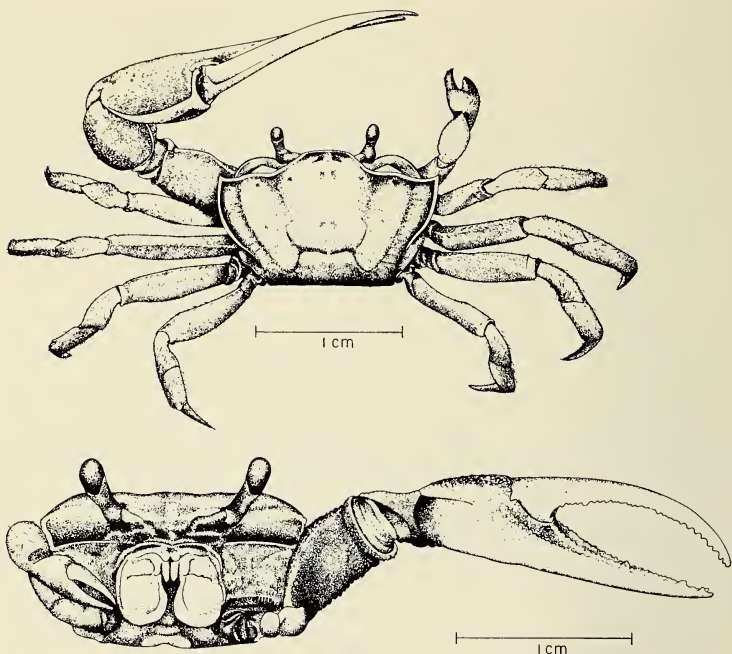


FIG. 2. *Uca panacea*, new species, holotype male. Top, dorsal view; bottom, frontal view.

tion of 4% formalin buffered to pH 7 with hexamethylenamine. Larval description is based primarily upon preserved specimens, although details were often checked against the morphology of living larvae.

***Uca panacea*, new species**

Etymology: Panacea, alluding to the location where this animal was first discovered.

Distribution: Specimens of *U. panacea* described here were collected from Saint Mark's Wildlife Preserve just east of Panacea, Florida. They are known to occur west to Texas (Selander, personal communication).

Types: Deposited in the Smithsonian Institution. Holotype, male, USNM 150096; allotype, female, USNM 150097; paratypes, 50 males, 50 females, USNM 150098.

Sample size: 250 preserved and 150 live animals of various sex and size combinations were used for this study.

Morphological description: (Figs. 1 and 2) Carapace moderately

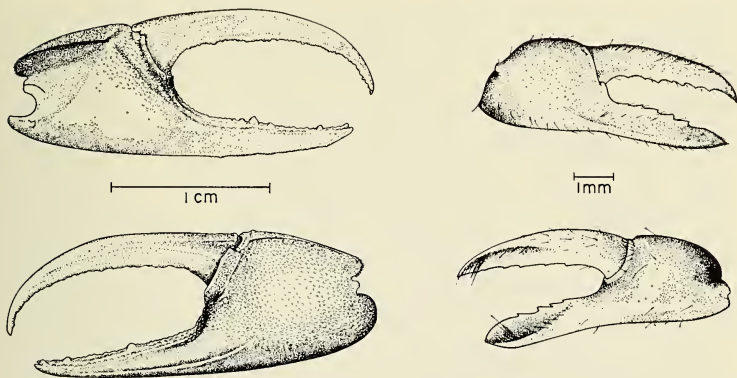


FIG. 3. *Uca panacea*, new species. Left, major cheliped: top, interior view; bottom, exterior view. Right, minor cheliped: top, exterior view; bottom, interior view.

arched, widest at anterolateral margins. Lateral margins parallel. Frontal margin transverse, angulate, forming obtuse angle on either side of protruding front. Surface of carapace smooth. H-form cardiac depression moderately outlined. Anterolateral margins distinct but blending into smooth surface of carapace posterior to middle of cardiac region. A ridge above last 2 pairs of walking legs on oblique lateral wall of carapace. Oblique and anterolateral margins converging anteriorly to form less than right angle. Carapace about 2.8 times wider than front but these proportions vary with size.

Minor cheliped (Fig. 3) slightly serrated along inner margin of lower finger except near flattened spoon tip. Distinct gap present when fingers are closed. Scattered row of hairs extending along margins of both fingers.

Outer surface of major cheliped (Fig. 3) smooth but covered with many small flat tubercles. Propodus about 1.30 times as long as dactylus but proportions vary with size. Dactyl 8.25 times as long as wide but proportions vary with size and maturity. Submarginal ridge on palm not developed and lacking distinct tubercles. Teeth of both fingers well developed. Inner row of teeth continuing along palm usually extending close to lateral margin of carpal cavity.

Carpus with oblique ridge on inner surface continuing proximally along upper margin of carpus with slightly developed tubercles to point of articulation with merus. Lower margin having distinct ridge containing tubercles extending proximally to point of articulation with merus.

Supplementary specific characteristics: (Figs. 4 and 5) Spoon-tipped hairs of second maxilliped totaling about 160, projecting beyond inner margin of merus with many more non-projecting shorter hairs. Hairs confined to wide zone on median and distal inner edge of merus. Spoon-

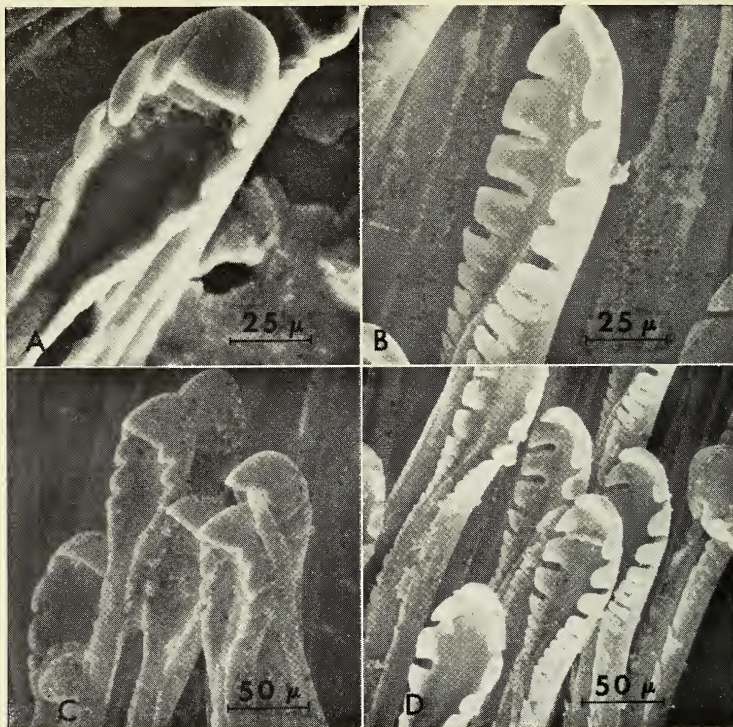


FIG. 4. Electron micrographs of spoon-tipped hairs from the second maxilliped. Left (A and C), *Uca pugilator*; right (B and D), *U. panacea*, new species. Note that tips are cup-shaped in the former, but more spatulate in the latter.

tipped process bearing 8-9 enlarged lateral lobes which continue as smaller lobes and extend down the shaft of the hair (Fig. 4).

Abdominal appendage with well developed arm. Curvature of tip continuing to follow that of shaft of appendage (Fig. 5).

Color: Carapace light grey-brown to uniformly creamy olive brown, being slightly darker posteriorly and laterally; the cardiac H-form depression is uniformly rust-red. Major cheliped of males white at fingers. Outside propodus orange to purple, palm usually being slightly lighter. Inner surface of carpus deep orange to red. Ambulatories white and speckled or uniform light red. Females with same color pattern. Color pattern of all animals altered with environmental conditions. Often carapace is considerably darker. When carapace is light colored, a pair of small grey spots can occasionally be seen slightly anterior to H-form depression.

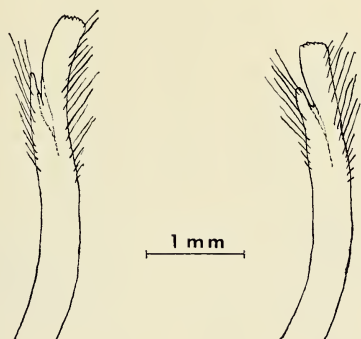


FIG. 5. Right abdominal appendage, seen from an anterior view. Right, *Uca panacea*, new species; left, *U. pugilator*.

Morphology of larvae: First zoea (Fig. 6-I); carapace dorsoventrally elongated, bearing dorsal and rostral spines. Rostral spine longer than dorsal. No lateral spines present. Carapace smooth with no sharp depressions or protuberances. Abdomen composed of 5 segments, 5th segment coalesced with telson. First abdominal segment predominantly covered by carapace. First and second segments show blunt lateral spines. Posterolateral margins of abdominal segments 2-5 overlap following segment with short blunt points, posterodorsal margin of each segment bears short hairs. Exopodite of maxilliped bears 4 natatory setae. Eyes sessile.

Second zoea (Fig. 6-II); carapace primarily unchanged with exception of slight protuberance just posterior to dorsal spine. Growth and expansion have occurred in carapace. Dorsal surface of first abdominal segment bears single setae centrally. Posterolateral edges of abdominal segments longer than in 1st stage and more heavily constructed. Exopodite of maxilliped bears 6 plumose setae. Eyes are now stalked.

Third zoea (Fig. 6-III); carapace enlarged with no apparent lengthening of dorsal and rostral spines over 2nd stage. Expansion of carapace gives dorsal spine stout appearance. Rostral spine still longer than dorsal. Carapace maintains smooth surface. Three setae appear in posteroventral margin of carapace; 3 setae are borne by, and are equally spaced along dorsal margin of first abdominal segment. First abdominal segment partially covered by carapace. Abdomen now composed of 6 segments, 6th bearing telson. Segments 3-5 have posterolateral projections which appear as short spines. Exopodite of maxilliped typically bears 8 plumose setae.

Fourth zoea (Fig. 6-IV); carapace remains smooth. Rostral and dorsal spines maintain previous size as carapace and abdomen continue to grow. First abdominal segment (hidden under carapace) bears 6

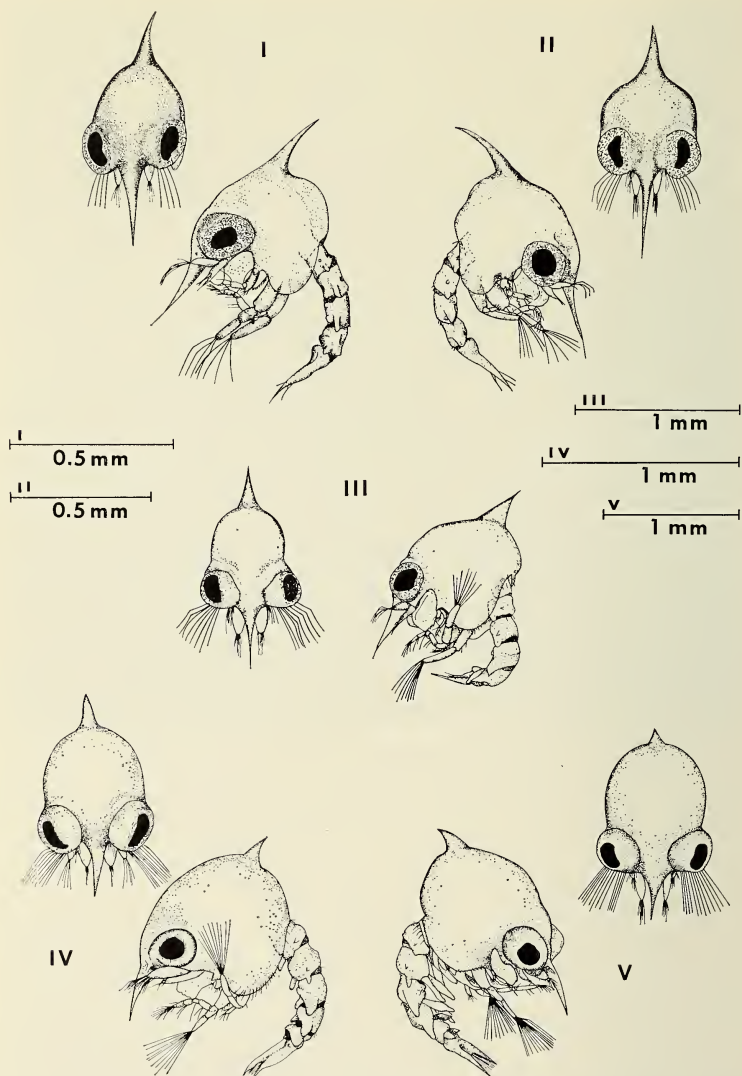


FIG. 6. *Uca panacea*, new species. Frontal and lateral views of the five zoeal stages.

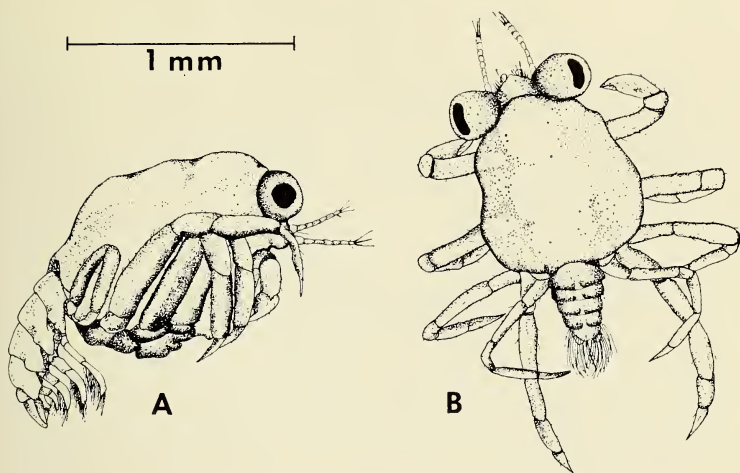


FIG. 7. *Uca panacea*, new species. Lateral (A) and dorsal (B) view of megalopa.

setae equally spaced along entire dorsal margin. Pleopod buds appear on abdominal segments 2–5. Spiny posterolateral projections on segments 3–5 are maintained. Maxilliped typically bears 10 plumose setae.

Fifth zoea (Fig. 6-V); carapace remains smooth. Eyes large, stalked. First abdominal segment (under carapace) bears 11 setae equally spaced along dorsal margin. Pleopods are more developed and occur on segments 2–5. Posterolateral margins of abdominal segments 3–5 have short spines which overlap following segment. Exopodite of maxilliped typically has 12 plumose setae.

Gross morphology of megalopa (Fig. 7); carapace oval when viewed from above, rounded on dorsal surface by 3 protuberances running from anterior to posterior surface. Chelipeds formed but small. Abdomen consists of 6 segments (1st segment hidden by carapace) plus telson. Segments 2–6 have bisegmented pleopods. Pleopods typically bear 15 setae each segment.

Gross morphology of first crab: (Fig. 8-A) Carapace round when viewed from above, extension of carapace between stalked eyes has formed. Depressions and protuberances slight and not well defined. Chelipeds are developed but small and equal in size. Abdomen (not visible in figure) carried under body where it fits into midventral depression.

Gross morphology of second crab: (Fig. 8-B) Carapace round when viewed from above, with grooves for horizontal reception of eyestalks. Extension of carapace between eyestalks now fully developed. "U"-

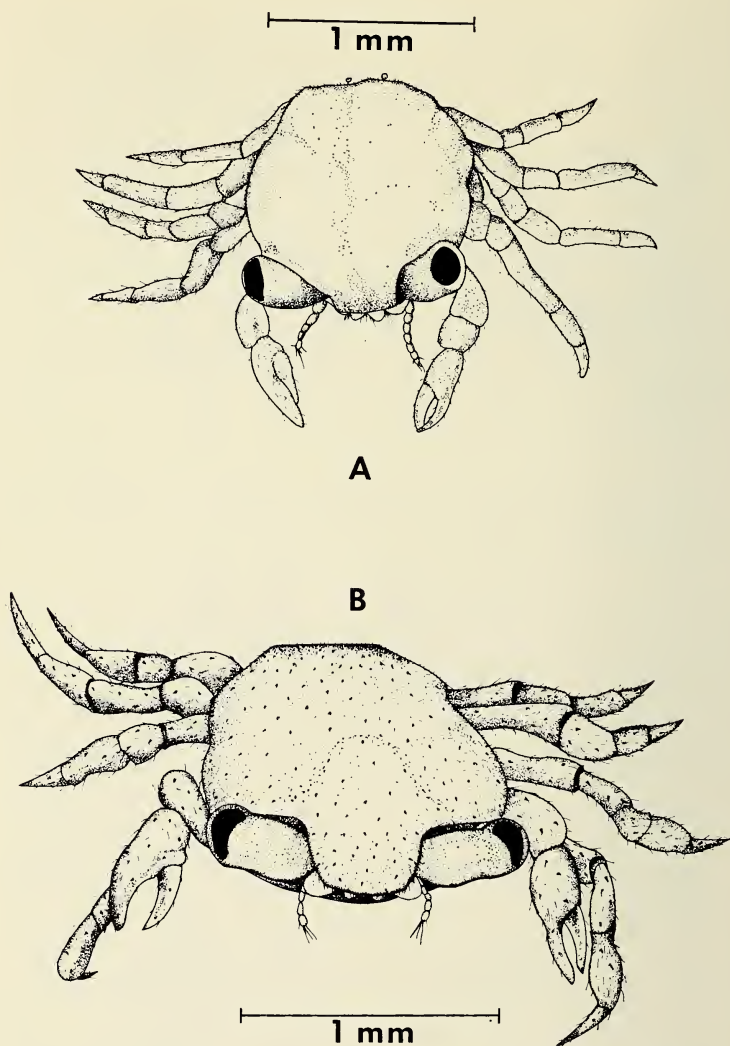


FIG. 8. *Uca panacea*, new species. A, dorsal view of first crab stage; B, anterodorsal view of second crab stage.

shaped slight depression sometimes apparent on dorsal surface of carapace, beginning posterior to eyestalks and arching posteriorly where arcs meet middorsally. Abdomen remains folded under ventral portion of body where it is retained in a depression.

COMPARISON WITH *UCA PUGILATOR*

While *U. pugilator* in the Carrabelle-Panacea area of Florida commonly reach a size greater than that of the largest *U. panacea*, the typical size of an adult *U. panacea* is in keeping with that of most mature *U. pugilator*. A typical carapace width for *U. panacea* in Carrabelle, Florida, is 1.6 cm, while *U. pugilator* commonly attains a width of 2.0 cm and occasionally larger. From a random sample of 500 animals collected, the greatest carapace width of *U. pugilator* was 1.91 cm while that of *U. panacea* was 1.63 cm.

Regressions were established using carapace width as a function of width of front. A random sample (20 of each sex for each species) was drawn and the regressions compared using F-test to establish whether the two regressions could be drawn from the same population. In both sexes the statistical analysis indicated that the slopes of the regressions of *U. panacea* ($b = 3.1088$, ♀♀, and 1.9254 , ♂♂) and those of *U. pugilator* ($b = 2.3674$, ♀♀, and 2.822 , ♂♂) were different (comparison of females: $F_{[1,36]} = 5.7771$, $p \leq .025$; comparison of males: $F_{[1,36]} = 7.2547$, $p \leq .01$).

Unfortunately, carapace pigmentation is variable within the two species. However, distinctive characteristics do exist in the form of the cardiac H-form depression, carpal pigmentation, the spots on the carapace and overall carapace color, especially when the animals are in a lightened state. A most distinctive characteristic is the rust-red cardiac depression on the back of *U. panacea*. This differs from *U. pugilator*, which typically has a dark grey-brown cardiac depression, and is maintained even when the animals assume the dark coloration.

Occasionally *U. panacea* is seen with a pair of small grey spots slightly anterior to the H-form depression. This marking is common in *U. pugilator* also, but two additional zones of purple pigmentation are located just anterior and lateral to the grey spots.

When animals assume light carapace pigmentation, differentiation becomes simple. *Uca panacea* appears creamy olive-brown compared to *U. pugilator* (creamy powder blue-grey carapace with deep purple spots). The difference in cardiac H-form is at a maximum then, with *U. panacea* bright rust-red compared to the greyish-brown of *U. pugilator*.

The broad flat inner margin of the carpus is orange to deep red in *U. panacea* and distinct from the rest of the appendage segments. The carpus of *Uca pugilator*, while having some red pigmentation, does not present as bright a color as in *U. panacea*.

The major cheliped of male *U. panacea* appears more slender than that of *U. pugilator*. Measurements confirmed this. Mean dactyl widths were compared between 15 crabs of each of the two forms, using a sample in which dactyl length was held between 1.55 and 1.59 cm. The mean $\pm s$ was 0.189 ± 0.007 cm for *U. panacea*, and 0.221 ± 0.006 cm for *U. pugilator* ($t = 191.3$, $p < .005$). Mean dactyl lengths were also compared, again using 15 crabs/sample, and holding carapace width

between 1.43 and 1.49 cm. For *U. panacea*, the mean was 1.51 ± 0.06 cm; for *U. pugilator*, 1.32 ± 0.14 cm. These values were also significantly different ($t = 131.4$, $p < .005$). Thus, in the major cheliped of *U. panacea*, the dactyl is more slender and longer than in *U. pugilator*. Of the 30 animals measured, the range and mean of the dactyl length: width proportion was 7.75–8.78, 8.25 for *U. panacea*; and 6.80–7.48, 7.09 for *U. pugilator*.

The overall proportion of dactyl length to propodus length is only slightly different between the two species. Regressions were established using dactyl length as a function of propodus length. With a random sample of 30 for each species, the comparison of slopes (*U. panacea*, $b = 0.864$, *U. pugilator*, $b = 0.800$) was not significant ($F_{[1,56]} = 2.3132$, $p < .10$). The tooth midway along the finger of the propodus is in most cases smaller in *U. panacea* than it is for *U. pugilator*.

Spoon-tipped hairs of both species are equal in abundance and distribution on the second maxilliped. In five *U. panacea* examined, 148–162 spoon-tipped hairs were counted extending beyond the inner margin of the merus. Crane (1943) describes *U. pugilator* as having 150–200 spoon-tipped hairs extending beyond the inner margin of the merus. Photographs under the scanning electron microscope however, indicate different morphology for the two species (Fig. 4). The spoon-tipped hairs of *U. panacea* are broader and shallower than those of *U. pugilator*. Lateral lobes of the former extend down the shaft of the hair, while in the latter, none are seen along the shaft.

Abdominal appendages of adult males are similar, but a difference is apparent in the angles and ridges at the tip of the appendage (Fig. 5). Six males of both species were compared. The appendage of *U. panacea* continues to follow the curvature of the shaft to the tip of the appendage, while in *U. pugilator*, it diverts away from the arm. This causes the tip of *U. pugilator* to form a concave arch on the side opposite the arm.

DISCUSSION

The larval as well as adult descriptions given here form a base of reference for species identification. The only previous description of larval development in *Uca* was done by Hyman (1922) for *U. pugilator*. Crane (1940) primarily refers to Hyman's description when comparing the Genus *Ocypode* to *Uca*. But Hyman did not rear his animals in the laboratory. Hence, his data are suspect, both in terms of uncontrolled environmental (salinity, temperature, nutrition) influences as well as species identification.

The distinct differences in the form of the spoon-tipped hair is of prime importance. According to Crane (1941), and Miller (1961), this character is correlated with feeding adaptations to different substrates. Thus the differences found here are indicative of niche specialization between the two forms.

Another important character, again indicative of species distinctiveness, is the difference in shape of the abdominal appendages. This slight

difference in form may, in conjunction with other adaptations, prevent interbreeding. No intermediate forms, which could indicate hybridization, were found in the field.

Color pattern is a distinctive characteristic differentiating the two species, and it is now known that fiddler crabs have color vision (Hyatt, 1973). Characteristics such as the bright color of the carpus on the major chela may coordinate vitally with the mating display of the male.

The description presented above indicates that *U. panacea* and *U. pugilator* are closely related and have probably diverged only recently. There is little doubt, based upon the combined evidence from this description and the biochemical study of Selander et al. (1971), that isolation is complete. The courtship displays of both species are also distinct and will be described in a separate paper. From an evolutionary viewpoint, this behavioral evidence must be considered the most conclusive for speciation (Crane, 1943; Cain, 1954; Mayr, 1966).

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